ACTIVE MOVEMENTS AND OTHER ASPECTS OF THE BIOLOGY OF ASTICHOPUS AND LEPTOSYNAPTA (HOLOTHUROIDEA) [1]

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The ability of certain benthic sea cucumbers to execute relatively rapid movements has not been generally recognized or given adequate treatment in comprehensive accounts of the Holothuroidea (*e.g.,* Ludwig, 1892; Cuénot, 1948; Hyman, 1955). In some bathypelagic species the performance of rapid progressive movements is regarded a normal means of locomotion. Ludwig (1892) and Hansen and Madsen (1956) have noted the remarkable swimming movements, first observed by M. Sars (1868), of *Bathyplotes natans* (=*Stichopus natans*), an aspidochirotid of the typically deep-sea family Synallactidae. Gilchrist (1920, p. 381) observed that ". . . some of the Holothurians procured in deep water off the South African coasts have the power of swimming about freely in the water by an undulatory movement of the body, ..." He further surmised that ". . . such deep-sea Holothurians do not bury themselves in the soft mud of the floor of the ocean, but flit more or less readily over its surface." More recently, Hansen and Madsen (1956, p. 55) have suggested, "Probably a power of swimming, though often awkward, may be attributed to a considerable number of Holothurians of the family Psychropotidae within the order Elasipoda and of the genera *Bathyplotes* and *Paelopatides* within the Synallactidae of the order Aspidochirota." These authors remarked that of the known bathypelagic holothurians, *Galatheathuria aspera* is probably the best adapted for active swimming, which in this species is effected through undulatory movements of the lateral brim much as in the swimming of the cuttlefish, *Sepia.* The elasipodid, *Benthodytes typica,* with a wide brim all around the body, is also well adapted for swimming.

Of the typically bottom-living, non-pelagic sea cucumbers, only a small number of species were known to execute relatively rapid movements. All of these species are members of the family Synaptidae in the order Apodida. As originally reported by Nutting (1919), and quoted by Fisher in Deichmann (1926), *Euapta lappa* can swim to a limited extent. Costello (1946) has described well the active, scissor-like movements of the young of *Leptosynapta albicans* (=*inhaerens*), as first reported briefly by Clark (1907, p. 63). Recently, Hoshiai (1963) has observed undulatory swimming in the young of *Labidoplax dubia*.

The quick swimming movements observed in adults of the aspidochirotid *Astichopus multifidus* and *Leptosynapta albicans* are documented for the first time in the present communication. Further, a description of some other kinds of locomotory movements performed by *Astichopus,* which were formerly unknown in the Holothuroidea, is included in this paper. Also, other aspects of the biology of *Astichopus* are investigated in relation to the species' active movements, *viz.* the nature of its habitat, the reactions elicited as a result of alterations of the immediate environment (for example mechanical disturbances, temperature, light, salinity), and its toxicity. A description of the sinusoidal swimming behavior of adult *Leptosynapta* concludes the study.

MATERIALS

Astichopus multifidus (Sluiter, 1910) is a member of the order Aspidochirotida; members of this group are characterized by possessing disk-shaped tentacles and respiratory trees. Examination of the structure of the gonad demonstrated that it occurs as two tufts, thus confirming that the species does belong to the family Stichopodidae (Deichmann, 1954). *Astichopus,* a monotypic genus in the West Indies, is easily recognized because it is very large and soft, with both dorsum and ventrum uniformly covered by hundreds of tube feet; the dorsal tube feet are papillate (Figs. 1 and 4). The dorsum of all specimens examined was some shade of brown or gray, and exhibited a variable color pattern. Two individuals had a chocolate brown dorsum with numerous small (*ca.* 1 cm. diameter) scattered white spots; the ventrum was also chocolate brown. Several specimens had a light brown dorsum, and one of these possessed in addition three large (3–5 cm. diameter), evenly spaced, chocolate brown spots. Lighter colored individuals tended to have a white ventrum. The tube feet and papillae were light in color, usually a translucent light yellow or light brown. Undisturbed, crawling *Astichopus* demonstrated a range in total length of 29–46 cm. Specimens observed by Clark (1933) were somewhat larger, at least 45 cm. in length. Aggregates of numerous minute grains and scattered C-, S-, or O-shaped calcareous particles occur in the body wall (Deichmann, 1954). Three of the specimens collected in Puerto Rico and used as material in this study have been deposited in the Smithsonian Institution, U. S. National Museum (Number E-10325).

Few specimens of *Astichopus* have been collected previously; the largest number reported were brought up in trawl hauls made on the Campeche Bank in the Gulf of Mexico. According to H. Hildebrand (quoted in Deichmann, 1954), this species is an abundant form in this region. Several specimens were also collected at Port Antonio, Jamaica, by Clark (1933). Since these earlier occurrences, no other specimens have been reported from Jamaica (Fontaine, 1953). This

species has been reported from only one other locality in the tropical western Atlantic, namely at Tortugas, Florida (Deichmann, 1963); the specimens found in Puerto Rico constitute a new record for this region. Because a dense population of this comparatively rare species has been discovered in Puerto Rico, an account of the habitat is given in the next section.

Leptosynapta albicans (Selenka, 1867), a well known Californian sea cucumber, belongs to the order Apodida, a group wholly lacking tube feet, and to the family

FIGURE 1. Underwater photograph of *Astichopus multifidus* at the edge of a bed of the seagrass, *Halophila baillonis,* in 15 m. of water at Crashboat Landing, Aguadilla (November 20, 1964). The length of this animal, as it is crawling in the picture, was approximately 35 cm. Forward progression is toward the right; visible are the cloacal aperture at the rear end of the animal to the left and a lateral fringe of papillae bordering the ventrum.

Synaptidae, whose members possess calcareous spicules in the form of anchors and anchor plates and tentacles with slender digits. The observations reported in this study were made on animals living in Monterey Bay, California.

Limited studies were carried out on *Synaptula hydriformis* (Le Sueur, 1823), a viviparous member of the Synaptidae. This is an abundant species of the West Indian fauna, usually living associated with algae. All specimens were collected from the red alga, *Laurencia papillosa,* which grows on a sandy bottom in the shade of red mangroves (*Rhizophora mangle*) on the reef flat at Cayo Májimo, La Parguera, Puerto Rico.

Because different methods were employed in the various experiments performed, these are discussed separately under the appropriate sections to follow.

Astichopus multifidus

Habitat

Astichopus has been found at five different localities in the coastal waters of western Puerto Rico (Fig. 2). It is most abundant on the northwestern coast, and at Crashboat Landing, midway between Pta. Borinquen and Aguadilla, several specimens have been observed on numerous occasions throughout the year. The species has been seen at depths of 20–40 m. at different times near Isabela, Camuy and Arecibo, and probably occurs in favorable localities between these areas.[2] The
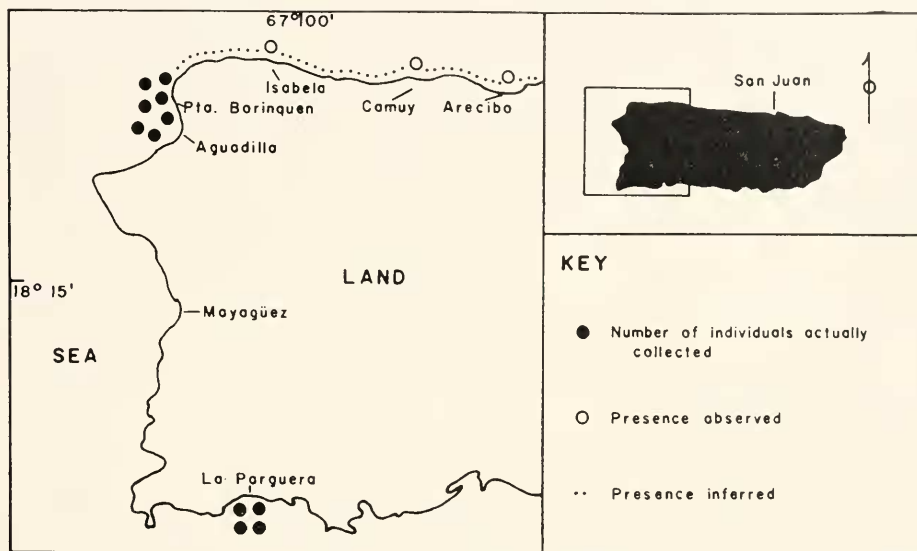

FIGURE 2. Map of western district of Puerto Rico showing the localities where *Astichopus* has been collected (solid circles) and observed (open circles) from June, 1960, to October, 1964. Its probable occurrence along the north coast is also indicated (dots). The small inset map of Puerto Rico shows the sector of the island examined.

results of a typical collecting trip to obtain specimens of *Astichopus,* conducted at Crashboat Landing on September 29, 1964, give an approximate indication of its abundance in this locality. Three individuals were found, two at a depth of 20 m. and one at 10 m. (measured with a wrist depth gauge), by two SCUBA divers swimming abreast, searching a path 10 m. in width over a distance of about 1 km.

A dense growth of the marine phanerogam, *Halophila baillonis,* was present where *Astichopus* was collected at 20 m.; the other specimen was taken from the bare sandy bottom. An underwater photograph of a cucumber on a *Halophila*-covered bottom is shown in Figure 1. The four individuals of *Astichopus* reported from La Parguera were found in the months of January, February, August and October at a depth of from 1 to 3 m., either on a bottom with a dense growth of turtle grass (*Thalassia testudinum*), or nearby on the bare sand on the leeward

[2] Gary E. Branham and Alfred H. Hummel informed the author of the occurrence of *Astichopus* at all localities from Pta. Borinquen east to Arecibo.

side between the two inshore coral reefs, Cayo Caracoles and Cayo Májimo. The present observations on the bathymetric range of *Astichopus* support Deichmann's (1963) belief that this species normally lives in deeper water, occurring at shallow depths only sporadically.

Other echinoderms observed commonly at Crashboat Landing on the sandy bottom between 30 and 45 m. of depth were the echinoids, *Astropyga magnifica* (Diadematidae) and *Meoma ventricosa* (Clypeasteridae). *Astropyga* is not reported from La Parguera and *Meoma* has been found there only infrequently.

Physically and biologically the shore line from Aguadilla to Camuy is decidedly different from that in the vicinity of La Parguera on the south coast. Kaye (1959) has described the northwestern coast, from Aguadilla to Arecibo, as largely composed of a limestone cliff, occasionally interrupted by a narrow rocky or sandy bench, which often forms a firm surface where cementation of dunes has occurred. Mangrove forests border most of the coastline around La Parguera and shallow fringing and patch reefs, composed of such prominent coral species as *Acropora palmata, Montastrea annularis* and *Porites porites* var. *furcata,* are numerous (Almy and Carrión, 1963).

Considerably stronger waves buffet the north coast of Puerto Rico than along the south shore, except during cyclonic disturbances from the southern quarter (Glynn, Almodóvar and González, 1964). The normally heavy surf along the north coast is a result of the following conditions: (a) this region is exposed directly to the high seas generated across the Atlantic Ocean, (b) the island shelf is narrow with few offshore reefs and banks, and (c) the windward shore receives large swells resulting from storms in the North Atlantic during the winter season (Kaye, 1959).

Substantial fresh-water discharge is also a prominent feature along the Atlantic seaboard of Puerto Rico. Because of the southern location of the north-south drainage divide, seven of Puerto Rico's 17 principal rivers, with an approximate drainage area of 1398 square miles or 64% of the total considered here, discharge at more or less regular intervals along the north coast (Arnow and Bogart, 1960). No permanent river system is present in the vicinity of La Parguera on the south coast.

Surface sediment samples (upper 5 cm. stratum), collected from the sites where *Astichopus* was found in greatest abundance at Crashboat Landing and Cayo Caracoles, vary considerably in grain size and composition (Fig. 3). The median diameters and degrees of sorting (as indicated by phi standard deviation; Inman, 1952) for the Aguadilla and La Parguera samples were 0.212 mm., with 1.1 phi-units and 0.392 mm., with 2.2 phi-units, respectively. The terrigenous fraction of the sample from Crashboat Landing contained mostly quartz and feldspar with about 5% heavy minerals. Calcareous bioclastic materials, constituting 97.2% of the dry weight of the sample from La Parguera, were nearly three times as great as at Aguadilla. *Halimeda* fragments were the principal constituents in the south coast sample, with the remainder composed of broken skeletons of other calcareous algae, the sessile foraminiferan, *Homotrema rubrum,* coral fragments, echinoid tests and spines and a variety of other invertebrate hard parts. The more poorly sorted sediment sample from La Parguera might be explained by the high per cent composition of plate-like *Halimeda* fragments and the location

of the area on the Caribbean Sea, in the lee of the heavy swells and surf action of the Atlantic coast of Puerto Rico. Sediment analyses reported by Guillou and Glass (1957) confirm the divergent character of the substrata as revealed in the present study. Calcareous and non-calcareous materials were observed to be present in equal amounts in the beach sands from Aguadilla to Río Camuy, while inshore sediments along the southwestern coast (all of south coast as shown in Figure 2) were predominantly calcareous.

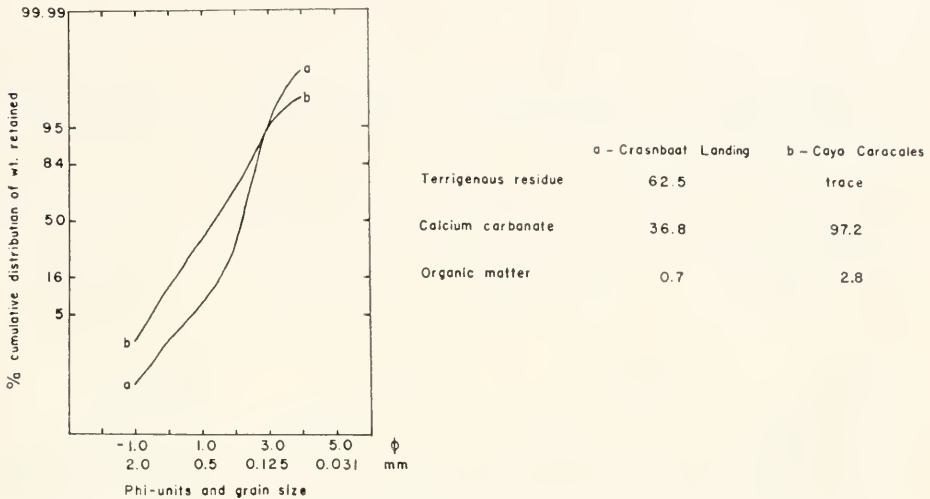|	a – Crasnboat Landing	b – Cayo Caracoles
Terrigenous residue	62.5	trace
Calcium carbonate	36.8	97.2
Organic matter	0.7	2.8

FIGURE 3. Plot on probability paper showing cumulative percent distributions of grain size in sediment samples from *Astichopus* habitats at Crashboat Landing, Aguadilla (a) and Cayo Caracoles, La Parguera (b). The per cent composition of the samples, based on dry weight, is tabulated in terms of terrigenous residue, calcium carbonate and organic matter content. Grain size distribution was determined by standard sieve analysis, calcium carbonate and organic matter contents by the difference in weights obtained after ample treatment with HCl and H_2O_2, respectively. The H_2O_2 technique employed is outlined by Stevenson and Emery (1958). Terrigenous residue, as here defined, was that portion of the sample remaining after the above treatment.

Movements

Clark (1933) observed that *Astichopus* is a very active form and remarked (p. 111) that it ". . . moved about more obviously than any other large holothurian I have ever watched." The various movements performed by *Astichopus* were studied in the field during daylight hours and in the laboratory during the day and at night. Animals maintained in captivity were kept in 200-liter DUROTEX (asbestos) troughs and 210-liter aquaria supplied with running sea water. Figure 4 illustrates some of the different movements observed, and the account of these follows.

A slow crawl is the most frequent means of progression when the animal is left undisturbed (Fig. 4a). All specimens observed in the field were crawling over the sandy bottom, ingesting the substratum by means of the circlet of large tentacles surrounding the mouth. Examination of gut contents showed that there

is no apparent discrimination of particle size, and that large fragments of either living or dead plant material are generally avoided. Two cucumbers, timed while crawling under laboratory conditions and not feeding, progressed at a mean rate of 0.25 and 0.15 m./min. (Table 1). Individuals observed in the field while feeding moved along at a slower rate. As indicated by the lengths measured in the two individuals included in Table I, a disturbed animal will contract to about three-quarters of its crawling length. When the body is contracted the dermal papillae (dorsal tube feet) are frequently withdrawn into the body wall. The
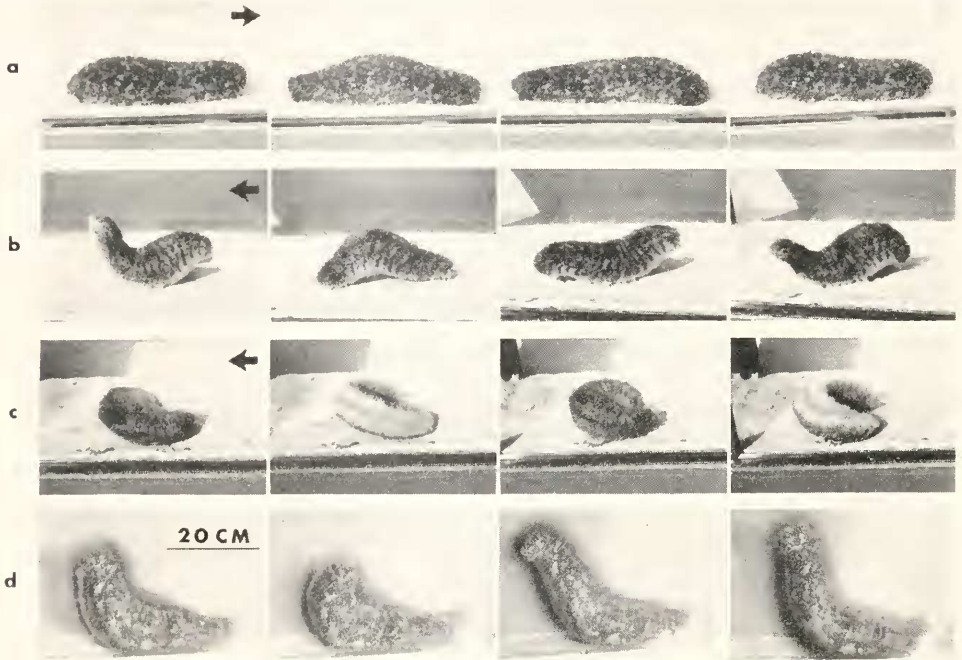

FIGURE 4. Four distinct movements performed by *Astichopus* in captivity. The four photographs in each horizontal series demonstrate (a) crawling, (b) bounding, (c) rolling and (d) an exploratory activity. Arrows in series (a) through (c) indicate the direction of forward progression, viewing the photographs in sequence from left to right. The inset scale in the first photograph in series (d) indicates approximately the sizes of the three different individuals illustrated. The actual lengths of the specimens, measured while crawling, were (a) 32 cm., (b) and (c) 30 cm., and (d) 46 cm.

crawl is accomplished through the forward progression of a peristaltic wave originating from the posterior end of the animal. The posterior end is first elevated two to four cm. from the substratum and then the wave moves forward, forming a two-cm.-high arch between the ventrum and the underlying surface. Of the many tube feet uniformly distributed over the ventrum, the few attached to the substratum are detached momentarily as the peristaltic wave moves forward. Three peristaltic waves passed across the body of a 40-cm individual in a mean time of 65 seconds. A second cycle is initiated by the time the first has moved over two-thirds of the body length.

Under certain conditions, to be discussed in the next section, the crawl will suddenly quicken to a walking or a bounding type of locomotion (Fig. 4b). A gradation in speed from crawling to bounding is clearly evident, but once one of the three modes of progression is executed it persists for some few minutes. Walking speeds of three-quarters to one m./min. are usual, whereas one and one-half to two m./min. are rates typical of the bounding movement (Table I). As in crawling, both walking and bounding are initiated by a peristaltic wave which moves forward along the body. However, the cycle is obviously more rapid and exaggerated at greater velocities. For example, in the bounding movement a wave passes along the entire length of the body in three to five seconds and there is no attachment of the tube feet to the bottom. As a wave terminates anteriorly, the forward end of the body is thrown upwards forcefully and at the same moment a new cycle begins at the hind end. Even at the highest speed attained, *Astichopus*

TABLE I

Rates of progression for the crawling, walking and bounding movements of
Astichopus as observed in captivity

Specimen	Type of movement (m./min.)		
	Crawling	Walking	Bounding
Light brown individual; crawling length	0.23	0.62	1.72
39 cm.; contracted length 30 cm.	0.25	0.76	1.89
	0.26	0.88	1.98
	$\bar{X}$ 0.25	0.75	1.86
Dark brown individual; crawling length	0.12	0.74	1.33
39 cm.; contracted length 32 cm.	0.16	0.90	1.43
	0.18	1.01	1.71
	$\bar{X}$ 0.15	0.88	1.49

always maintained contact with the bottom. Indeed, it appears that this contact is necessary for the forward thrust, since animals pushed over on their sides and still bounding remain essentially stationary. Many of the dorsal papillae contract into the skin while the animal is walking or bounding. The total distance covered by one specimen while bounding in an aquarium was about 10 m. Each time the animal reached the obstructing wall at the end of the aquarium it was turned around gently so as not to interfere with its forward progression. Animals walking or bounding tended to deviate little from a straight-line course. Only limited bounding movements have ever been observed in the field, *i.e.*, of the order of one to one and one-half m. traversed at a time.

A swimming-like response was observed by Cutress (personal communication) on one occasion. The animal actually left the bottom and progressed through the water in an undulatory manner. Further attempts were made to repeat the act, but they resulted only in the bounding movement already described. In the present study one individual on two different occasions was stimulated to bound in the field by subjecting the animal to a sudden change in the temperature of the

water (see section on environmental effects on movements), but the bounding movement did not lead to swimming.

Rolling movements also occur frequently, and as shown in Figure 4c the body flexes into a U during this activity. A complete roll is carried out in unison along the whole length of the animal. About one-half of the dorsal papillae are contracted during this movement. One individual made several complete rolls in a mean time of five seconds. Rolling may last as long as five minutes, with the animal moving little from its original position. It became evident that all of the movements thus far described were less easily evoked in individuals recently stimulated and in some animals activity decreased in frequency and intensity with time maintained in captivity.

An exploratory or searching activity was observed on only one occasion (Fig. 4d), and this occurred in one of three individuals in the same aquarium immediately after transportation to the laboratory from the field. About one-third of the anterior portion of the body was elevated, and this swung frequently from side to side, describing an arc of approximately 40°. A full swing to the left is shown in the second photograph in Figure 4d. The exploratory movements lasted for about 10 minutes and culminated in the erect posture illustrated in photographs three and four of Figure 4d. With over one-half of the body in an upright position the animal bowed forward several times, forming an angle of 45° from the vertical.

The five longitudinal retractor muscles, which must play an important role in all of the various movements, are very well developed in *Astichopus* as 1–2-cm.-broad bands running the length of the body. Comparable muscles in a closely related, sluggish form, *Isotichopus* (= *Stichopus*) *badionotus,* are thin and narrow. The body wall is tough and thick in both species, but soft and pliable in *Astichopus* and rigid in *Isostichopus.* Excessive muscular development has also been reported in the swimming sipunculid, *Sipunculus natans* (Fisher, 1954), a member of a typically benthic group. This species has developed strong longitudinal muscle bands and enormous wing-muscles.

Environmental effects on movements

In order to learn how the various movements just described may be used to advantage by *Astichopus,* several animals were stimulated in the field and in the laboratory to produce disturbing circumstances likely to be encountered by the species in its natural surroundings. Such conditions studied were various bodily disturbances, alterations in the temperature of the water, reduction in salinity, effects of oxygen-deficient water and behavior in numerous divergent light regimes. In all instances parallel control procedures demonstrated that the movements evoked were due to the particular conditions under investigation.

Procedure involving mechanical stimulation was as follows. Two individuals were buried completely beneath the bottom sediments and elevated quickly (in 30 seconds) toward the surface, over an ambient pressure gradient of one atmosphere. All of the animals responded by contracting initially, then after a minute or two began to crawl. Gentle handling of specimens normally produces the same reaction. All of several individuals, turned over on their dorsa and sides, righted themselves immediately, in 3–5 seconds, by the rolling movement. A half- or quarter-roll only was performed to regain normal posture. Since current action

on the bottom is relatively strong at Crashboat Landing, often swaying the animals from side to side down to a depth of 30 m., this quick, righting response is well suited to help maintain proper orientation.

Sudden changes in sea water temperature, of the order of 3–4° C., elicited the walking, bounding and rolling movements more effectively than any other environmental alterations investigated. To test the effects of temperature, animals were moved rapidly from one aquarium, at a lower or higher temperature, to another. In addition, some individuals were maintained in a slightly cooled or heated state in captivity, and then transferred rapidly to the field. The laboratory sea water temperatures ranged from 27.5° to 29.3° C. over the duration of the experiments. Coastal sea water temperatures at this time of the year (October) were in the range of 27–29° C. Different individuals of *Astichopus* were subjected to the following typical changes in temperature: from 29.1° C. to 32.4° C., and from 27.7° C. to 23.3° C. Essentially the same movements were performed when the animals were subjected to a temperature which was greater or less than the initial temperature. Immediate bounding was the most frequent response, lasting for one to three minutes. A rolling movement was less common, while walking was observed on relatively few occasions. Once a particular type of movement began it usually persisted until the animal slowed down to a crawl.

The behavior of *Astichopus* under different conditions of lighting was investigated with the following light sources: natural daylight, house light (tungsten filament lamp), red light (infrared lamp), yellow light (sodium lamp), filtered green light, blue light (mercury lamp) and violet light (ultraviolet lamp). The light beam was directed so as to enter a 210-liter aquarium on one side from above; cucumbers were placed lengthwise along the edge of the lighted portion and the shadow of the dark side of the aquarium, which was covered with black cloth. Observations were made in a darkroom where the light intensities employed were equal to or less than 10 foot-candles. Light intensities up to 75 foot-candles were measured with a Weston photoelectric cell (Model 703, sight meter); an estimation of greater illumination was obtained by the interposition of green filters over the photocell and by calibrating the Weston meter against a General Electric Mascot exposure meter (Type PR-35).

Individuals showed a marked attraction to natural and artificial light of low intensity ($\leqq$5 foot-candles), by immediately crawling toward the source. No consistent phototactic attraction or repulsion could be discerned at higher light intensities of 10, 20, 30, 50 and even 11,000 foot-candles (zenith sun at noontime in November). Usually, however, activity did increase at higher illuminations. In contrast to the usual photo-negative response of holothurians (Crozier, 1915) *Astichopus* crawled with equal frequency toward and away from the illuminated end of the aquarium. The phototactic behavior of *Astichopus* seemingly parallels that of *Isostichopus,* a form not apparently irritated by a strong source of illumination.

Monochromatic light was adjusted so that a maximum intensity of 10 foot-candles entered through one side of the aquarium. *Astichopus* demonstrated a strong, positive attraction to red, green, blue and violet light; individuals moved toward the light immediately by crawling and lingered in the region of greatest illumination. Only a modest attraction to yellow light was observed.

Astichopus did not demonstrate any clear tendencies in geotactic or thigmotactic behavior. Animals climbed readily up and down the vertical sides of containers and surfaces inclined at various angles to the horizontal. Occasionally individuals in the field were found alongside submerged pipes and pilings. Movements of confined laboratory animals indicate, however, that the association with solid objects may occur simply by chance wandering.

Effects resulting from a reduction in salinity were observed in the laboratory in individuals transferred from the sea water in which they were maintained to tanks containing sea water diluted with tap water. The normal, mean, surface salinity on the inshore reefs of the south coast for November, when these particular studies were made, was around 34.50‰ (unpublished data). Experimental dilutions were 31.00‰ and 17.25‰. Animals suddenly subjected to these conditions usually contracted, but occasionally executed a bounding motion. An equal intensity of reaction, in terms of speed and duration, was noted in both dilutions.

Individuals of *Astichopus* were also transferred to oxygen-deficient sea water—obtained directly over anaerobic mud on the floor of a mangrove canal. Of the rapid movements a bounding response was elicited most frequently under these conditions; limited rolling was also observed.

The possibility that the association of *Astichopus* with members of its own species or with other organisms may elicit active movements was also investigated. Individuals together in the same container behaved independently, *i.e.*, they crawled about as if alone and tended to avoid contact with other cucumbers. Animals introduced into an aerated aquarium in which *Astichopus* was previously living showed no signs of excitation. The water in this case was recirculated through a filter instead of being replaced by fresh, running water. Simulated biting, by firm pinching of different regions of the body with the bare hand, was observed both in the field and in the laboratory. This evoked a typical contraction of the body with subsequent crawling after 1–2 minutes. Introduction of a fresh slime preparation from the skin of *Lactophrys bicaudalis*, a trunk-fish which regularly preys on the small holothurian, *Microthele* (= *Holothuria*) *parvula*, in the immediate vicinity of *Astichopus* also failed to produce any active movements.

Two observations indicated that *Astichopus* might possibly possess a toxic substance that adversely affects other organisms nearby. *Petrochirus diogenes*, a large scavenging and possibly predatory hermit crab (Randall, 1964) found in association with *Astichopus*, tended to avoid the cucumber in captivity. In addition, several fishes in the same aquarium with *Astichopus* died after one cucumber eviscerated.

Toxicity

Yamanouchi (1955) has clearly demonstrated that numerous species of holothurians are toxic; of 27 species investigated, 24 contained a venomous substance. Nigrelli and Jakowska (1960) reported that poisonous species are known in four of the five orders comprising the class; members of the deep-sea order Elasipodida have not been examined in this connection. The total number of species of cucumbers known to be toxic to fishes is 30—24 of these live in the Pacific Ocean, three in the Mediterranean and four in the West Indies (Bahamas). One of the latter

species occurs in the Mediterranean and in the West Indies. The toxic principle in the common Bahamian species, *Actinopyga agassizi*, has been identified as a saponin, a chemical structure previously unknown in the animal kingdom (Nigrelli *et al.*, 1955).[3]

Investigations were made of the possible adverse effects on other marine animals of (a) the water in which *Astichopus* had recently performed active movements, (b) its coelomic fluids, and (c) alcohol extracts of the body wall. Freshly killed cucumbers were used in all instances. The potency of *Astichopus* was assayed by observing the effects produced in seven species representative of six different animal phyla: Coelenterata, Madreporaria—*Porites porites* var. *furcata* Lamarck, 1816; Annelida, Polychaeta—*Hesione proctochona* Schmarda, 1861; Mollusca, Pelecypoda —*Lima scabra* Born, 1778; Arthropoda, Crustacea—*Mithrax* (*Mithraculus*) *sculptus* (Lamarck, 1818); Echinodermata, Ophiuroidea—*Ophiothrix angulata* Say, 1825; Chordata, Tunicata—*Ecteinascidia turbinata* Herdman, 1880; Chordata, Pisces—*Jenkinsia lamprotaenia* (Gosse, 1851). All of the invertebrate species were held in wide-mouth bowls with one liter of aerated sea water at a temperature of 28–29° C.; *Jenkinsia* was held in a circular bottle of 10 liters capacity. All invertebrates except *Ecteinascidia* were collected on the same day of an experiment from the south shore of Magueyes Island, in association with the fringing *Porites porites* var. *furcata* reef. *Ecteinascidia* was collected from mangrove roots bordering the canal which separates Magueyes Island from the mainland; *Jenkinsia* was netted near the shoreline of the same canal. Parallel control material, with at least the same number of individuals observed as in experimental, always accompanied each experiment.

Two 10-ml. samples of sea water, taken from separate 5-liter containers in which one *Astichopus* had rolled and another bounded, did not produce any visible effects on the test animals over a 24-hour period.

An unsuccessful attempt was made to stimulate evisceration in three different individuals by firmly squeezing and pinching various areas of the body. Further, evisceration did not occur under the diverse experimental conditions to which *Astichopus* was subjected. Only two individuals eviscerated over a two-month period and the cause was not readily apparent. Much of the gut and the respiratory trees were ejected; Cuvieran organs are unknown in all Stichopodidae. For these reasons, it does not appear likely that evisceration is a normal defensive response. The body fluids tested for toxicity, then, were obtained by dissection from the coelomic cavity. Undiluted coelomic fluid, equal to a final concentration of 1000 ppm. (parts per million), was added to the water in which the test species were confined, and their reactions observed continuously for the first two hours after introduction and then at 4 hours and 8 hours. At the termination of the experiment animals were transferred to running sea water for a duration of 12 hours in order to observe recovery. The various responses noted are summarized in Table II.

Polyps of the scleractinian coral *Porites* contracted slightly in the first one-half hour and remained in this state for 8 hours. In 4–8 hours a mild lethargic response was observed in *Hesione, Mithrax* and *Ophiothrix;* they all became less

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[3] Studies on the chemical nature of the toxic agent are presently being carried out by the author in collaboration with Horace Graham, Department of Biology, University of Puerto Rico, Mayagüez.

irritable to mild mechanical stimulation. *Lima* reacted immediately by violently closing its valves; after about one hour they began to gape. By two hours the water became noticeably reddened and contained numerous small fragments of mantle tissues voided by the animals. *Ecteinascidia* responded by slowly contracting until at 8 hours all individuals were dead; cessation of heart beat was used as a criterion of death. *Jenkinsia*, the small clupeid, perished quickly; two fish were

TABLE II

*Observations of the effects on some marine animals of the body fluids of
Astichopus at a concentration of 1000 parts per million*

Organism	Number observed	Reactions at indicated time intervals					Recovery (12 hrs.)**
		½ hr.	1 hr.	2 hrs.	4 hrs.	8 hrs.	
Coelenterata *Porites porites* var. *furcata*	3 terminal branches, over 100 polyps in each	polyps slightly contracted	same	same	same	same	yes
Annelida *Hesione proctochona*	3	normal*	normal	normal	loss of quick wriggling response	same	yes
Mollusca *Lima scabra*	5	immediate and complete closure of valves	valves open in 2 individuals	all open; small bits of mantle tissue ejected	same	same	yes
Arthropoda *Mithrax (Mithraculus) sculptus*	4	normal	normal	normal	loss of quick defensive reaction of chelae	same	yes
Echinodermata *Ophiothrix angulata*	5	normal	normal	normal	normal	sluggish	no
Chordata-Tunicata *Ecteinascidia turbinata*	1 colony of 20 individuals	normal	siphons slightly contracted	same	siphons and body wall contracted	all dead; siphons and body wall greatly contracted; no heart beat	—
Chordata-Vertebrata *Jenkinsia lamprotaenia*	5	normal	2 dead	all dead	—	—	—

* A normal reaction indicates that no difference could be discerned between the test animals and controls. Same applies to Tables III and IV.
** Twelve hours in running sea water were allowed for recovery after the termination of the experiment. Same applies in Tables III and IV.

dead at the end of the first hour and all five had succumbed in two hours. The five control individuals of *Jenkinsia* lived beyond the 8 hours of the experiment. Recovery occurred in four of the five surviving species; *Ophiothrix* died.

Yamanouchi (1955) and Nigrelli and Jakowska (1960) have extracted with hot ethanol an active, toxic principle from the body wall of various holothurians. Alcohol extracts obtained from *Astichopus* were prepared as follows. A one-inch square of the body wall was macerated in a mortar with 30–40 mesh quartz sand. The mash and juices were then treated with 50 ml. of 95% hot ethanol at 50–60° C. for 10 minutes. The extracts at concentrations of 1000 and 5000 ppm. were tested

after cooling to room temperature. The results are presented in Tables III and IV.

The reactions of the test animals to alcohol extracts were very similar to those resulting from exposure to body fluids. Usually, however, a more severe reaction was evoked by the extract when equal to or at a greater concentration than the body fluids. The slightly contracted polyps of *Porites* after one hour were completely withdrawn in two hours. Lethargy again occurred in *Hesione, Mithrax* and *Ophiothrix*. Additional effects observed after 8 hours were inflation of the

TABLE III

Observations of the effects on some marine animals of an alcohol extract of the body wall of Astichopus at a concentration of 1000 parts per million

Organism	Number observed	Reactions at indicated time intervals					Recovery (12 hrs.)
		½ hr.	1 hr.	2 hrs.	4 hrs.	8 hrs.	
Coelenterata *Porites porites* var. *furcata*	3 terminal branches, over 100 polyps in each	normal	polyps slightly contracted	polyps fully contracted	same	same	no
Annelida *Hesione proctochona*	5	normal	normal	normal	loss of quick wriggling response	body inflated; proboscis everted	yes
Mollusca *Lima scabra*	5	active swimming followed by complete closure of valves	valves partially open; tentacles constricted	small bits of mantle tissue ejected	moribund	all dead	—
Arthropoda *Mithrax (Mithraculus) sculptus*	5	normal	normal	normal	loss of quick defensive reaction of chelae	same	yes
Echinodermata *Ophiothrix angulata*	5	normal	normal	sluggish	same	autotomy of arms	no
Chordata-Tunicata *Ecteinascidia turbinata*	1 colony of 20 individuals	normal	siphons and body wall slightly contracted	same	same	siphons and body wall greatly contracted	no
Chordata-Vertebrata *Jenkinsia lamprotaenia*	5	erratic swimming followed by death in 10 minutes	—	—	—	—	—

body and eversion of the proboscis in *Hesione* and extensive autotomy of the arms in *Ophiothrix*. Violent swimming movements were executed by *Lima* in the first few minutes, followed by closure of the valves. Individuals began to open after 1–2 hours; the pallial tentacles were noticeably shortened and constricted; reddened water, apparently due to the leakage of blood through ruptured tissues, appeared after two hours. All specimens of *Lima* succumbed during the experiment. *Ecteinascidia* responded by severe muscular contraction and cessation of heart beat at a concentration of 5000 ppm. Rapid, erratic swimming commenced in *Jenkinsia* immediately, resulting in the death of all specimens within 10 minutes. The gills were reddened in fish subjected to a concentration of 5000 ppm., indicating hemorrhage of the capillaries. A similar cause of death was observed in

the killifish, *Cyprinodon baconi,* after exposure to an aqueous preparation of the toxic agent of *Actinopyga agassizi* (Nigrelli, 1952). Five species survived and two recovered from exposure to the extract at 1000 ppm., whereas of the four surviving species at 5000 ppm. only the majid crab, *Mithrax,* recovered.

TABLE IV

Observations of the effects on some marine animals of an alcohol extract of the body wall of Astichopus at a concentration of 5000 parts per million

Organism	Number observed	Reactions at indicated time intervals					Recovery (12 hrs.)
		½ hr.	1 hr.	2 hrs.	4 hrs.	8 hrs.	
Coelenterata *Porites porites* var. *furcata*	3 terminal branches, over 100 polyps in each	normal	polyps slightly contracted	polyps fully contracted	same	same	no
Annelida *Hesione proc-tochona*	5	normal	normal	less active	sluggish; loss of quick wriggling response	body in-flated; proboscis everted	no
Mollusca *Lima scabra*	5	active swim-ming fol-lowed by complete closure of valves	valves tightly closed	2 dead; 3 moribund; valves par-tially open; small bits of mantle tissue ejected	4 dead; 1 moribund	all dead	—
Arthropoda *Mithrax (Mithra-culus) sculptus*	3	normal	normal	normal	loss of quick defensive reaction of chelae	same	yes
Echinodermata *Ophiothrix angulata*	5	normal	normal	sluggish	same	autotomy of arms	no
Chordata-Tunicata *Ecteinascidia turbinata*	1 colony of 20 indi-viduals	normal	siphons and body wall slightly contracted	all dead; siphons and body wall greatly con-tracted; no heart beat	—	—	—
Chordata-Vertebrata *Jenkinsia lamprotaenia*	5	erratic swimming followed by death in 10 minutes; gills reddened	—	—	—	—	—

LEPTOSYNAPTA ALBICANS

On three different occasions over the period January-May, 1957, four adult in-dividuals of *Leptosynapta albicans* were observed swimming at night light stations in Monterey Bay, California. During that time of year, night light stations were occupied at approximately weekly intervals. All observations were made on dark nights, between 9:00 and 11:00 PM, from a float secured to the Monterey Municipal Pier. The sea bottom is sandy below the float and about 7 m. deep (measured

from mean sea level).[1]   The direction of swimming was along the outer border of visibility illuminated by a 200-watt lamp suspended in the water—about three m. away from the observer.

The swimming animals described a sinusoidal path as they moved through the water near the surface (Fig. 5). It was not possible to determine whether the progressive waves of activity occurred in the lateral or dorso-ventral plane. While swimming the cucumbers were extended in length to about 20 cm., but when captured quickly contracted to about 5 cm. It is estimated that a complete wave passed from the head to the tail end in about two seconds, and that the animals
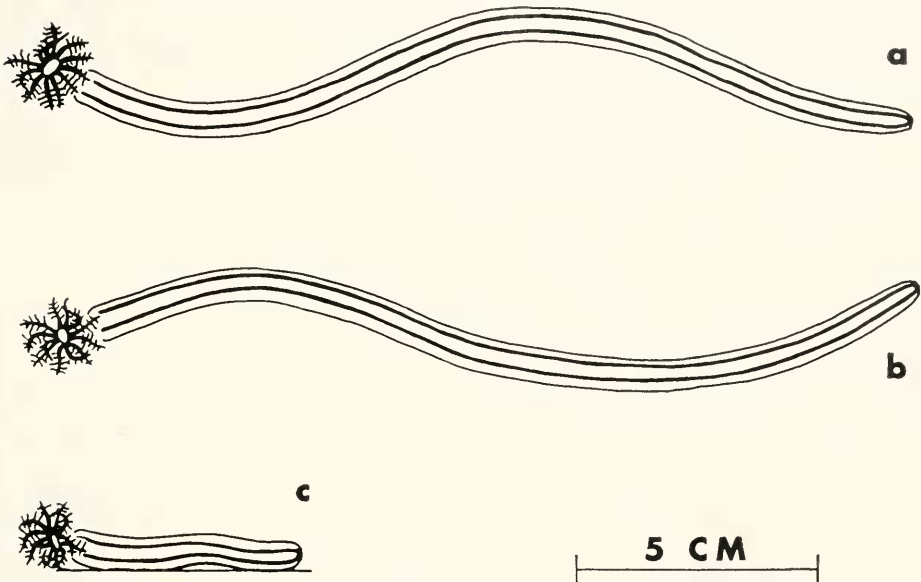

FIGURE 5. Diagrams of the undulatory swimming movements performed by *Leptosynapta* in the field (a and b) and the more frequent appearance of the animal when crawling (c).

moved through the water at a rate of one meter per minute. Individuals appeared to move in the direction of the tentacular crown, although this requires verification. Participation of the tentacles in swimming appeared insignificant. Hoshiai (1963) observed that *Labidoplax* turns its anal end in the direction of movement. Like the swimming young of *Leptosynapta* (Costello, 1946) and *Labidoplax*, captured adult *Leptosynapta* did not void an appreciable amount of fecal material. Three specimens dissected open showed no signs of recent gonadal activity.

All netted specimens were transported to the laboratory and maintained in an aquarium with running sea water. To induce swimming the same animals were treated in the following ways: (a) maintained in natural and total darkness, (b) subjected to sudden changes in light intensity (the most severe of these involved transfer from a dark room to direct sunlight), (c) dropped through a four-foot column of water, (d) subjected to a sudden increase or decrease of water tempera-

[1] This area has not been re-examined since the construction of a nearby breakwater and small craft shelter.

ture ($14 \pm 4°$ C.), (e) subjected to electric shocks (three graded series of voltages at 1, 10 and 100, each delivered at frequencies of 1, 10 and 100 per second), (f) subjected to a sudden increase in concentration of acid (HCl) or base (NaOH); two to three drops of 18 N HCl and a saturated solution of NaOH (ca. 30 N) were introduced separately into one end of a small pan containing the cucumber. An attempt was always made to keep deleterious stimuli at a sublethal level. None of the above treatments elicited a swimming response. In most cases the cucumbers tended only to avoid the stimuli by contracting the body and tentacles.

Since swimming movements have been reported for three species of apodid holothurians, *Synaptula hydriformis*, a readily available species belonging to the same group, was also investigated. Stimuli identical to those enumerated above were administered to several individuals of *Synaptula*. In addition, a fresh slime preparation from the skin of the trunk-fish, *Lactophrys bicaudalis,* was introduced into an aquarium containing several individuals of *Synaptula*. The sea water temperature during the experiment was $28 \pm 4°$ C. As in *Leptosynapta*, none of these treatments prompted a swimming or otherwise active response. The reactions were similar to those observed by Olmsted (1917), involving muscular contraction of various parts of the body.

Discussion

It is of interest to contrast the habitat of *Astichopus* in Puerto Rico with that portion of the Campeche Bank in the Gulf of Mexico where the species also occurs in abundance. Numerous specimens are commonly encountered in the shrimp grounds on the Campeche Bank, from a few fathoms down to a depth of 20 m. The location of the shrimp grounds in this region (Hedgpeth, 1954, p. 206), when compared with Lynch's (1954, p. 79) map of the sedimentary provinces, shows that the bottom deposits are essentially muddy. The usually muddy and estuarine conditions where shrimps are found along the Gulf coastal states, including a high organic matter content, contrast notably with the environment of the north coast of Puerto Rico. However, there is evidence that the faunal composition of the more southern shrimping grounds is decidedly different from that in the northern Gulf (Hedgpeth, 1953, 1954), perhaps reflecting significantly different physical and chemical properties of the environment as well. Kornicker et al. (1959), who compiled a list of the biota of Alacrán Reef, located near the center of the Campeche Bank and away from muddy deposits, did not report the presence of *Astichopus* or the seagrass, *Halophila*.

The relationship between grain size and the distribution of benthic feeding types suggests a further complication in an attempt to delineate the set of environmental factors favorable to the species. Sanders' (1958) findings, that clay is a good sediment correlate in the distribution of deposit-feeding organisms, would seem to apply where *Astichopus* occurs in very fine sediments on the Campeche Bank. However, McNulty et al. (1962), in agreement with the present findings, observed that deposit feeders were most abundant in sediments with a median grain size of about 0.25 mm. On the other hand, individuals of *Astichopus* with a dry body weight (excluding ingested materials) of the order of 100 gm. do not lie on the curve relating body size to grain size proposed by McNulty and co-workers for deposit feeders. According to their findings, which show a linear relationship be-

tween grain size and the cube root of dry tissue weight, one would expect *Astichopus* to occur in sediments with a median grain diameter in excess of 0.8 mm. The delicate and highly dendritic structure of the tentacles and the way these are employed in ingesting fine sediments indicate that feeding may be more efficiently executed on fine-grained substrata.

Deichmann (personal communication) has observed that many species of cucumbers go shorewards during the breeding time. However, the four individuals of *Astichopus* found in shallow water in La Parguera did not have the gonads in an active condition. Possible breeding in the late autumn or early winter is suggested by the occurrence of a 5-mm. *Astichopus* in shallow water in the Bahamas in May (found by C. Fernández Mosher). La Parguera specimens were collected in the winter, summer and autumn seasons. The present scanty records indicate that the occurrence of *Astichopus* at shallow depths is not associated with breeding.

The walking, bounding, rolling and erect exploratory movements of *Astichopus* represent newly-described activities for the benthic Holothuroidea. Even the relatively slow crawl of this highly active species is rapid compared with other forms. The mode of crawling in *Parastichopus parvimensis* (Parker, 1921) resembles very closely that in *Astichopus,* but individuals of nearly equal size progressed at a rate of only 1 m./15 min., or 0.07 m./min., equivalent to one-fourth to one-half the speed in *Astichopus.* Peristaltic waves pass along the bodies of the two species at the same rate, *viz.* at mean times of 63 seconds in *P. parvimensis* and 65 seconds in *Astichopus.* In *Parastichopus* one peristaltic wave at a time passes over the body; in *Astichopus* a second cycle begins before the first has ended.

The swimming movements of the species *Bathyplotes natans* were described by M. Sars (Hansen and Madsen, 1956) as similar to those of swimming leeches. The snake-like bends of the body occurred in the dorso-ventral plane, not side-wise. Assuming that the progressive peristaltic waves were initiated from behind in *Bathyplotes* (in leeches the waves pass back along the body from the head) it is possible that the swimming observed in *Astichopus* by Cutress is very similar to that reported by Sars.

A speed of nearly 2 m./min. attained by *Astichopus* when bounding, approaches the greatest velocities observed among echinoderms, *viz.* comatulid crinoids, 5 m./min.; *Centrostephanus longispinus* (echinoid), 2.1 m./min.; *Crossaster papposus* (asteroid), 2 m./min.; ophiuroids, 1.8 m./min. (Hyman, 1955). Prosobranch gastropods, which, like sea cucumbers, progress by means of peristaltic waves, are considerably slower; one rapid crawler, *Thais rustica,* attained a maximum velocity of 0.3 m./min. (Coomans, 1961).

The fast movements performed by *Astichopus* may actually facilitate a more rapid adjustment to certain adverse conditions encountered naturally. As pointed out earlier, a rolling movement is used by the cucumber for stabilization in strong currents. The method by which a bounding movement could help *Astichopus* avoid conditions of high temperature stress is suggested by the following possible circumstances. Reactions to light and gravity indicate that *Astichopus* is capable of moving readily into shallower or deeper water. Also, this species is very sensitive to a sudden change in the sea water temperature; such a change will immediately evoke a bounding response. Protected, shallow bodies of water heat up considerably during mid-day low water phases of the tide in the summer. For

example, on one occasion in La Parguera a temperature difference of 8° C. was observed between shoal water on the lee side of a reef (36° C.) and the surf zone to windward (28 ° C.). A cucumber wandering into such heated shallows could possibly escape the high temperature if the bounding movements were executed and properly directed. Abrupt changes in temperature are probably not so frequently experienced where *Astichopus* occurs at greater depths. Bathythermograph curves, obtained from stations located slightly less than one mile west of Pta. Borinquen, show that a distinct thermocline occurs as deep as 90–120 m., with a temperature gradient of 3° C. over about 7 m. (Gilbert Bane, personal communication).

Bounding sometimes resulted under experimental conditions when animals were suddenly subjected to reduced salinities and oxygen-deficient water. Although ample data are not available on the patterns of salinity and oxygen distributions around the river mouths on the north coast, aerial views show turbid river discharge extending seaward 2–3 miles and as streaks up to 5 miles along the coast. The effects of such conditions on populations of *Astichopus* will be the subject of a future investigation.

Aside from an exploratory type of behavior, observed on only one occasion in captivity (in the presence of two other animals), active movements are not elicited in *Astichopus* through association with members of its own species. Exposure to the juices of a possible predator (*Lactophrys bicaudalis*) also failed to arouse the cucumber. Sund (1958) likewise could not demonstrate that certain supposed predatory starfishes were responsible for quick swimming movements performed by the actinian, *Stomphia coccinea*.

Water in which *Astichopus* had performed movements did not have a toxic effect on other animals, thus showing that increased activity does not cause the release of a toxic substance. The coelomic fluid caused death in a species of brittle star, tunicate and fish at a concentration of 1000 ppm. However, the likelihood that body fluids are released naturally does not seem great, since *Astichopus* is not inclined to eviscerate even under extreme irritation. Alcohol extracts of the body wall proved to be more toxic than the coelomic fluids; five of the seven species tested perished at a concentration of 1000 ppm. Yamanouchi (1955) concluded that the poisons contained in holothurians apparently have little ecological significance. Though the toxic principle is confined largely to the tissues of the cucumber, a possible role of influencing the activities of other animals through diffusion of trace amounts into the surrounding water, for example in averting potential predators, cannot be dismissed.

Costello's (1946) description of nocturnal swimming by the young of *Leptosynapta* has dispelled the common notion that this species passes its entire postplanktonic life completely buried in soft bottoms (Hyman, 1955, p. 209). Moreover, the undulatory swimming movements performed by adult *Leptosynapta* show that Costello's suggestion is not true, namely that (1946, p. 95) ". . . *Leptosynapta* swims only during a limited period of its young adulthood." The scissor-like body flexures in the swimming young are entirely different from the sinusoidal undulations which move across the entire length of the body in adults. In addition, the movements of the young were described by Costello as more or less aimless, with

a velocity of 5–6 cm./min., whereas in adults swimming was directed and occurred at a velocity of about 1 m./min.

Specimens of *Labidoplax dubia,* like adult *Leptosynapta* species, also swim in an undulatory manner (Hoshiai, 1963). Curiously, though, this species holds its anal end highest and toward the direction in which it is moving. *Labidoplax* swims from early June to late July during any lunar phase, but only after darkness; swimming begins one hour after sunset and ends one hour before sunrise. By inducing several individuals to swim in the dark during the day, Hoshiai clearly substantiated Costello's idea that swimming in synaptids is a dark-conditioned phenomenon. Darkness and a variety of other experimental procedures did not elicit swimming in adult *Leptosynapta.* It does not seem likely that the swimming behavior is related to spawning, since the gonads showed no signs of being in a ripe condition or recently spent. Furthermore, Runnström observed that *Leptosynapta albicans* erects itself only part way out of the burrow when spawning (Hyman, 1955, p. 176). In the light of present knowledge no definite statement can be made about the stimulus that evokes swimming in synaptids or the possible benefit received.

SUMMARY

1. Aspects of the biology of the aspidochirotid, *Astichopus multifidus* and the apodid, *Leptosynapta albicans,* studied in Puerto Rico and California, respectively, were investigated in relation to the active movements performed by these species.

2. *Astichopus* is present in greatest abundance between 10 and 40 m. of depth on the northwestern coast of Puerto Rico. It often occurs in or near beds of the marine phanerogam, *Halophila baillonis.* Sandy beaches, cemented dunes, and beach rock, exposed to the heavy seas of the Atlantic Ocean, make up the shoreline of this region. Numerous large rivers loaded with terrigenous materials discharge on the north shore. The sediment on which *Astichopus* lives is comparatively fine-grained (median diameter = 0.212 mm.) and well sorted ($\sigma_\varphi = 1.1$); the terrigenous component is high (62.5%), calcareous bioclastic materials occur in substantial amounts (36.8%), and the organic matter content is low (0.7%). A smaller number of *Astichopus* has been collected from shallow water (1–3 m.) in the winter, summer and autumn at La Parguera on the south coast.

3. In addition to a comparatively fast crawl, forward progression in *Astichopus* is executed by rapid walking and bounding movements, which in the latter case may approach a rate of 2 m./min. Rolling and exploratory movements are also performed by *Astichopus.*

4. Mechanical stimulation usually causes *Astichopus* to contract for 1–2 minutes. Walking, bounding and rolling movements are elicited by sudden changes in the temperature of the water, of the order of 3–4° C. A positive phototactic response occurs at low light intensities ($\leqq$5 foot-candles); phototaxis increases at higher light intensities, but no definite negative response is apparent. A strong positive attraction to red, green, blue and violet light is evident at a low intensity of 10 foot-candles. No clear tendencies were noted in geotactic or thigmotactic behavior. Bounding movements sometimes occurred when cucumbers were suddenly subjected to diluted sea water and oxygen-deficient water. Active movements were not evoked through the association of *Astichopus* with members of its own species or in the presence of other animals.

5. Coelomic fluids and alcohol extracts of the body wall of *Astichopus* are toxic to a variety of marine animals at concentrations of 1000–5000 ppm. It does not seem likely that a poison is released by the animal naturally, since the water in which active movements are performed is non-toxic and evisceration occurs only rarely.

6. Sinusoidal swimming movements were observed in adult *Leptosynapta* on three different occasions near the surface at night. Specimens subjected to a variety of experimental conditions in captivity failed to elicit the swimming response. *Synaptula hydriformis*, a related West Indian species, did not swim either when subjected to diverse stimuli as with *Leptosynapta* or when exposed to the juices of a presumed predatory trunk-fish.

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